Review

Biogeography and ecology: towards the integration of two disciplines

Robert E. Ricklefs[1],* and David G. Jenkins[2]

[1]*Department of Biology, University of Missouri-Saint Louis, One University Boulevard, Saint Louis, MO 63121-4499, USA*
[2]*Department of Biology, University of Central Florida, Orlando, FL 32816-2368, USA*

Although ecology and biogeography had common origins in the natural history of the nineteenth century, they diverged substantially during the early twentieth century as ecology became increasingly hypothesis-driven and experimental. This mechanistic focus narrowed ecology's purview to local scales of time and space, and mostly excluded large-scale phenomena and historical explanations. In parallel, biogeography became more analytical with the acceptance of plate tectonics and the development of phylogenetic systematics, and began to pay more attention to ecological factors that influence large-scale distributions. This trend towards unification exposed problems with terms such as 'community' and 'niche,' in part because ecologists began to view ecological communities as open systems within the contexts of history and geography. The papers in this issue represent biogeographic and ecological perspectives and address the general themes of (i) the niche, (ii) comparative ecology and macroecology, (iii) community assembly, and (iv) diversity. The integration of ecology and biogeography clearly is a natural undertaking that is based on evolutionary biology, has developed its own momentum, and which promises novel, synthetic approaches to investigating ecological systems and their variation over the surface of the Earth. We offer suggestions on future research directions at the intersection of biogeography and ecology.

Keywords: history; macroecology; niche; phylogeny; regional community; species sorting

1. INTRODUCTION

The speakers in this symposium were paired to contrast different perspectives on issues of common interest. Although ecology and biogeography had a common origin in nineteenth-century natural history, these disciplines grew apart with their formalization and the search for mechanisms to explain patterns early in the twentieth century [1]. For example, the experimental tools of genetics and population biology were useful for studying the adaptations of organisms and the regulation of populations, but did not readily apply to global patterns of distribution and diversity. The schism possibly peaked during the 1970s, soon after Robert MacArthur [2,3] explicitly excluded history from the purview of ecology, which the historian of science Sharon Kingsland [4] referred to as 'the eclipse of history.' Indeed, one could argue that ecologists further weakened the study of biogeography through the development of the equilibrium theory of island biogeography, which was essentially non-historical [5,6], and with hypotheses to explain variation in species richness by local, primarily ecological, mechanisms [7–9], and, more recently, the promotion of stochastic mechanisms lacking ecology, including

mid-domain effects [10,11] and neutral community theory [12,13].

Only after the general acceptance of plate tectonics in the 1960s and the development of increasingly analytical approaches to studying geographical distributions, such as panbiogeography [14], vicariance biogeography [15], analytical biogeography [16] and areography [17], did biogeography experience a resurgence that eventually commanded the attention of ecologists [18] including the development of macroecology [19–21]. It is worth noting in this context that several ecological societies were founded early in the twentieth century (British Ecological Society, 1913; Ecological Society of America, 1915), whereas the Journal of Biogeography dates from 1974 and the International Biogeography Society (IBS) was established only in 2000. Despite its slow start, however, activity in biogeography is rapidly increasing, and the discipline is converging with organismal ecology, which is itself becoming more regional in scope [22]. The common ground of biogeography and ecology has become a compelling area for exploration, but the terrain remains poorly mapped. The purpose of our symposium at the 2011 meeting of the IBS was to promote discussion towards this end by bringing together biologists with different perspectives on common themes.

The contributions to this symposium appearing in this issue emphasize the increasing integration of biogeography and ecology, as well as lingering differences

remaining to be bridged. Beyond this, we offer some personal observations on the contemporary relationship between these disciplines, emphasizing the current trend towards their unification. The common ground uniting two disciplines is perhaps best understood by first charting their differences. From the most general considerations, biogeography and ecology have been distinguished by their disparate foundations of (i) language and tradition, (ii) data and experimental/analytical tools, and (iii) scale and perspective (from the standpoint of both time and space). Modern ecology addresses mechanisms responsible for pattern and relies heavily on experimental approaches, which limit the spatial and temporal scale of processes that can be investigated. Biogeography has been concerned with large scale, indeed global, patterns in the distributions of populations and in the diversity of natural systems. The relevant processes are also primarily large in scale (species production, vicariance) or infrequent (long-distance dispersal) and often historically contingent (major extinction events, plate tectonics). Naturally, data and methods diverge at the extremes, as does language. Each discipline has used a different vocabulary for its unique phenomena and processes. But different disciplines also use the same words in different ways; terms such as *distribution*, *community*, *dispersal* and *niche* often have different meanings when applied by biogeographers and ecologists. For example, to many biogeographers 'dispersal' applies to the colonization of a new area, and thus the expansion of a species' distribution, but ecologists often think of dispersal in terms of the movement of individuals within a population influencing local demography and genetic differentiation. Of course, the same word also can mean different things to different people within the same discipline; 'community' and 'niche' are good examples [23–26].

2. LANGUAGE AND USAGE
As Weiher *et al.* [27] emphasize, we are held hostage by words as much as we are empowered by them. For example, the word 'community', as it has been used in ecology, might refer to an entity (for which the existence of boundaries has been a persistent source of disagreement) or to a concept that embodies the effects of interactions among species [25]. By attaching the word 'community' to an assemblage of species within a defined study area, one is encouraged to believe that the local presence and absence of species reflect interactions occurring within the area. In ecology, this way of thinking has promoted research on the rules of community assembly based on the ability of species to coexist locally. Problems with words like 'community' partly reflect perspective, for example, characterizing local assemblages by presence versus abundance of species. Presence or absence of a species in a location is a useful indicator of species distributions in regional-scale studies (e.g. [28,29]), whereas abundance, reflecting more subtle habitat qualities and species interactions, might be more appropriate for ecological studies at local scales. However, while experimental ecology has demonstrated the influence of local species interactions on populations (e.g. [30]), these interactions alone do not determine the presence and

relative abundance of species locally. 'Community' is a conceptually useful term that can be applied to all ecological systems, but has informed theory primarily in closed systems (i.e. those that neither receive nor export organisms), as in the Lotka–Volterra equations for competition and predation. This community concept struggles with the more open systems that we confront as ecology approaches biogeography, requiring that species interactions be given a spatial context. The word 'meta-community' [31,32] represents an effort to consider local communities in a regional context and may be treated as a sample [29] of a regional community [25]. The progression towards more regional perspectives in community ecology reflects past frustrations with communities perceived as empirical entities that can be defined spatially [25]. This inadequacy of language is indicated by ecology's long interest in measures of diversity [33] and spatial turnover (beta diversity; [34]); both attributes address the overlap and similarities among communities. Even the word 'assemblage', often used in place of 'community' [35], conveys a sense of organization and an underlying set of processes.

Chase & Myers [34] make a similar point about 'niche' being one of those terms that defy definition but appear familiar when seen. Of course, each viewer 'sees' niches with different eyes. As in the case of 'community', the term 'niche' is more useful as a concept related to an individual's (Eltonian niche?) or a species' (Grinellian niche?) physical place and functional role in the environment [24]. Hutchinson's [36] multi-dimensional niche axes (e.g. prey size, soil pH, temperature, etc.) further emphasize that 'niche' might be more useful as a concept than a measurable entity, especially when it is measured in a single, local context but varies among locations within a species' range.

The way we talk about niches influences our thinking and our science. Species are often shown in ecology texts as being evenly distributed along niche axes with a minimum of overlap, representing the idea of niche partitioning. In neutral theory, however, species are not distinguished ecologically and niches overlap completely. Where does nature lie on this continuum? Should the way we portray species' niches vary with geographical or ecological scale? Wiens [37] points out that we have little basis as yet to consider the concept of the ecological niche at the spatial and temporal scales of biogeographers. How different are fundamental and realized niches, and is there a consistent relationship between them? Biogeography needs to better reconcile large-scale patterns with ecological niche concepts, though it is difficult to address such basic issues without first letting go of some of the traditions we have inherited while working at traditional scales in biogeography (or ecology). In this way, future careful articulation of concepts and research at the intersection of both disciplines can transform each discipline.

3. DATA AND ANALYSES
Progress in science tends to follow paths of least resistance, and those paths meander in time. Particularly at large dimensions of size and complexity, we are limited by data and analytical approaches, and we tend to use

what is available. Chiarucci *et al.* [33] address the task of quantifying species diversity and biodiversity and point out choices between using phylogenetic and functional diversity, whether to weight species abundance, and the relevance of species versus landscape diversity. In a very practical sense, quantifying biodiversity in a way that is useful for conservation and management depends on the goals of biodiversity management. We must also keep goals in sight when we answer more basic questions concerning the origin and maintenance of patterns of biodiversity. The growing availability of data and analytical power in ecology and biogeography has made possible the global analysis of patterns of mammal species richness and phylogenetic diversity described by Davies & Buckley [38]. However, the rush to the global scale carries the risk of abandoning, to some degree, local scales where biogeography, ecology and evolutionary adaptation intersect. Thus, we find it intriguing that global analyses (e.g. [38]) point to regions of particular interest for both basic and applied biodiversity work in the future. We also note that the emphasis on global *pattern*, which is becoming increasingly accessible, does not necessarily resolve the issue of underlying *process*, which becomes more complex as scale increases.

The analysis of the ancestral relationships of species based on DNA sequences (phylogenetic analysis) has greatly stimulated analyses in ecology and biogeography by opening a window on the historical dimension. In addition, phylogenetic relationship has been adopted as a proxy for functional relationship (distance in niche space, perhaps), enabling large-scale analyses of species sorting and niche partitioning, discussed in §7. Four papers in this issue represent this general approach, which will continue to forge an important link between biogeography and ecology. Davies & Buckley [38] use phylogeny to interpret the history of diversification of mammals in different parts of the world, and distinguish recent rapid radiation of a few groups from the retention of many ancient diverse lineages. Smith & Lyons [39] use phylogenetic relationship to distinguish convergent evolution from common ancestry in the interpretation of size distributions of mammals. Emerson *et al.* [40] employ phylogenetic analysis to explore the contributions of colonization and local diversification to species assemblages and illustrate how molecular genetics methods have also become essential tools for quantifying diversity itself in poorly known taxa. As Poulin *et al.* [41] point out, interpreting comparative ecology in a phylogenetic context can be difficult in host–parasite systems where the two players are linked to each other, but phylogenetic context is essential to tease apart patterns and better infer processes.

4. SCALE AND PERSPECTIVE

The most persistent theme in the continuum between biogeography and ecology is that of scale in time and space, from the individual organism and its lifetime activities (local scale) to population distributions (mesoscales and beyond) to clades that diversify across geographical regions (global scale; [22]). To some degree, constructed patterns at small and large scales can be connected analytically by beta diversity or distance decay in similarity [34,41–43]. Distance decay

reflects underlying processes, among which dispersal limitation and local adaptation have received attention. To use distance decay in ecology and biogeography will require that it be explicitly scale-specific and, ultimately, that distance decay patterns be compared across spatial scales. To do so implies organized data collection and analysis at multiple scales, and comprises a potentially fruitful and challenging research agenda. Outcomes of such research may find a common denominator among diverse scales and thus aim towards strong and valuable predictive capacity. Although such commonalities across scales are possible, it is clear that ecological processes probably dominate mechanisms at local, short-term scales, while evolutionary processes dominate at global, long-term scales. This expectation does not deny that evolution happens in 'ecological time' [44] but simply suggests inverse gradients in the signal-to-noise ratio of ecological and evolutionary processes across temporal and spatial scales. The intersection of those gradients at intermediate temporal and spatial scales represents the regional-scale intersection of ecology and biogeography.

Community ecology, biogeography and evolution reflect local-scale outcomes of the properties and actions of individuals, including genetics and the epigenetics of individual development. The link between evolutionary change in populations and variation in individual fitness exemplifies this connection between scales. The expression of natural selection depends, of course, on the environmental context (that is, pattern at a larger scale), and evolutionary change overall depends as well on chance. It is not clear, however, to what extent the expression of natural selection is rational—that is, comprehensible—at a higher level. In the case of evolution, we can interpret the outcome of this unfolding of process into pattern (adaptation) in the context of our understanding of fitness. Although we probably would not predict a kangaroo *a priori*, we can at least, having become aware of its existence, understand why it is the way it is in terms of the mechanics of locomotion. Nonetheless, the world outside Australia seems to have functioned perfectly well without kangaroos (although some rodents evidently are kangaroo wannabes). Clearly, kangarooness itself is not predictable from the environmental context at a larger scale, but can only be rationalized *a posteriori* from general principles of adaptation.

The distributions of populations are like the qualities of kangaroos, unpredictable in most respects but possibly rationalized after the fact in terms of physiological and biochemical adaptations to the physical environment, the distributions of competitors, predators and pathogens, and other contexts. Kangaroos and population distributions obey many laws of nature, but are historically contingent on past influences. Distributions of species living in the same environment vary immensely in location, extent and local density. More over, although probabilities of population persistence and diversification might represent a fitness criterion in biogeography, it is nonetheless difficult to rationalize distributions as qualities of populations. Where distributions have been analysed in a phylogenetic framework, 'heritability' (evolutionary conservatism) of individual population qualities typically is low [45–47]. As a

result, we expect that predictive, niche-based models of species distributions (e.g. [48]) will be all the more interesting when combined with detailed genetic analyses and common garden experiments to test for heritable variation in fitness. Also, overlapping combinations of such models for multiple species may be one means to bridge the gap between species-specific adaptive regimes and community ecology, consistent with regional communities [25].

5. BIOGEOGRAPHIC PATTERN
As shown in the contributions to this symposium issue, patterns do emerge in biological systems. For instance, ecologists, evolutionists and biogeographers have long shared a common interest in convergence—similarity in form and function arising from disparate origins. For example, convergence explains the similar appearance and functioning of Mediterranean-type vegetation in distant parts of the world [49–51]. Body-size distributions of mammals also are similar across zoogeographical realms, suggesting common constraints on the evolution of size and perhaps size-dependent packing of species into available ecological space [39]. Some patterns of distribution and diversity also exhibit convergence: for example, the latitudinal gradient of diversity appears to be independently derived in the Old World and the New World. Parallelism between regions also suggests common independent outcomes: the range extents of disjunct herbaceous plant genera shared between eastern Asia and eastern North America provide a geographical example [52]; correlations in species richness (but not species identity) of plant families between Eastern and Western Hemisphere forests [46] additionally suggest parallelism in diversification.

Equally important are cases that lack parallelism or convergence, which can highlight mechanisms that apply uniquely in different places. Classic examples are differences in diversity of forest trees in similar environments in America and Europe, generally attributed to selective extinction of European species with climate cooling and glaciations during the late Tertiary [53–55]. In this example, the unique geography of Europe, with the Alps and Mediterranean Sea forming east–west barriers to southward range shifts, suggests the precedence of history and large-scale processes over local ecology in regulating diversity. The greater species richness of mangrove plants in the Indo-West Pacific compared with the Western Hemisphere [56,57] is another example, possibly attributable to a greater propensity for the evolutionary origin of mangrove lineages in areas with shallow seas and isolated islands, characteristic of the early Tertiary Tethys region and, more recently, the Indo-Malayan region, but largely lacking from the Western Hemisphere [58].

Biogeography is practised in considering large-scale patterns like those above, but modern ecology has been considered ergodic (i.e. invariant and ahistorical; [1]) and rarely considers such effects, in part because we study ecological systems within regions and less often confront pattern at larger scales. As McIntosh ([1], p. 6) wrote 'The question for ecologists is: Are there any ergodic properties in ecological phenomena?' As ecologists begin to invoke historical/biogeographic processes to reconcile different patterns within and among regions (e.g. [59]), they will hasten the unification of ecology and biogeography.

6. PHYLOGENETIC THINKING
Phylogenetic reconstruction has opened a window onto the history of contemporary patterns. As elaborated by Emerson *et al.* [40], phylogeography portrays the geographical history of genetic diversity within or among closely related species and can elucidate the history and direction of colonization. Species phylogenies, especially those calibrated with respect to time, allow certain inferences about the origins of large-scale patterns, including areas of origin and the spread of diversity. Based only on taxonomic data, botanists have understood for decades that plant clades characteristic of high latitudes are generally nested within larger clades with primarily tropical distributions [60]. This pattern is consistent with the broader distribution of tropical climates during the Late Cretaceous and Early Tertiary, and suggests that high-latitude diversity has been constrained by both time and barriers to adaptation imposed by stressful conditions [59,61–64]). This evolutionary inertia, which apparently has prevented so many tropical lineages from leaving home, is commonly referred to as 'tropical niche conservatism' [65–68].

Writing in this issue, Davies & Buckley [38] contrast a measure of the phylogenetic diversity of mammals, which takes into account the timing of diversification and contemporary species richness to elucidate aspects of the history of diversity. Although Africa holds more ancient evolutionary lines of mammals—reflecting the early origins there of most mammal lineages—South America has undergone more rapid recent radiation, particularly with the Late-Tertiary introduction of additional old mammal lineages from North America (the Great American Interchange) [69–71] and, to a lesser extent, as in the case of platyrrhine primates (New World monkeys) [72,73] and caviomorph rodents [74,75], by overwater dispersal from Africa [76]. A similar approach has revealed that tropical areas generally hold more ancient lineages and also support more rapid diversification in many groups (e.g. [76,77]).

Phylogenetic relationship has also been used to infer processes involved in the distribution of species *within* regions. Two processes have opposite influences. On the one hand, related species share traits that are adaptive to certain parts of the environmental space (e.g. portions of the spectrum of temperature, precipitation, soil mineral composition or climate seasonality). In G. E. Hutchinson's terms [36], related species tend to share portions of their fundamental niches, that is, the range of conditions under which they are able to persist in the absence of impacts from other species. Consequently, assuming that close relatives tend to share traits (evolutionary conservatism), one would expect to find related species living together. On the other hand, related species have similar resource requirements and at a more local scale might exclude one another through the depressing effect of competition on population growth. In this way, the realized niches of related species within their shared

fundamental niche space would overlap less than expected at random [78,79]. In a phylogenetic analysis, one would expect fewer close relatives living together at *small* spatial scales, but more than the random expectation at *large* spatial scales, and this is a common result of phylogenetic community analyses (e.g. [80,81]). This tension between phylogenetic trait similarity (clumping) at large spatial scales and differentiation (overdispersion) at small scales is a theme discussed in this issue by Emerson *et al.* [40], Wiens [37], Weiher *et al.* [27] and Chase & Myers [34] illustrating the current and broad-based focus on evolutionary/phylogenetic information in judging the balance between local and regional processes. Though we expect this general approach will evolve in method, phylogenetic thinking is fast becoming the norm in research conducted at regional and local scales and will continue to be important at the biogeography–ecology intersection.

7. SPECIES SORTING AND NICHE PARTITIONING
Ecological species sorting at large scales and community assembly at small scales potentially provide rules governing some of the distribution and diversity patterns observed in nature. In this case, the production of species through large-scale processes, which forms the regional species pool, is balanced by processes at two levels: adaptation to different parts of the environment (species sorting) and interactions between species (niche partitioning). Much of classical community ecology has addressed niche partitioning and community assembly (see [27,34]), but the interplay between species interactions and local diversity needs further consideration. Weiher *et al.* [27] emphasize the value of focusing on species functional traits as a way to bring greater clarity to community assembly, in contrast to community assembly research that has focused on species composition. Species traits and phylogenetic signal (e.g. [82]) will become an increasingly valuable approach to reveal species sorting and niche partitioning in community assembly at regional scales.

Community assembly emphasizes ecological (habitat) filtering, species interactions and random processes; the first two are niche oriented, that is, referring to the species fundamental niche (phylogenetic clumping) in contrast to the realized niche resulting from partitioning ecological space (phylogenetic overdispersion) [83–86]. Emerson *et al.* [40] place ecological neutrality, representing processes that create pattern in the absence of ecological distinctions between species [12] in a central position between ecological species sorting and niche partitioning, on the one hand, and history and geography, on the other. Weiher *et al.* [27] also place neutral processes and outcomes between species sorting and niche partitioning. It is interesting to consider, in this sense, whether the appearance of neutrality in many situations reflects the absence of ecology (i.e. neutrality *per se*) or a balance between the opposing ecological forces of ecological sorting and competitive exclusion at intermediate spatial scales. Presumably, neutrality would be indicated when the degree of phylogenetic relationship among species sampled locally would not differ significantly from a random draw from the regional

species pool, potentially leading one to conclude that species are distributed independently with a region. This emphasizes the importance of examining relationships across scales, but begs the question of what proportion of the variation in species distributions can be attributed to associative or dissociative influences, and at what spatial scales. This question also may help direct a greater role for ecological niche concepts in biogeography, given that those concepts have not been fully incorporated yet [37].

8. SATURATION OF ECOLOGICAL SPACE
Ecologists have not resolved whether ecological space is filled by species to capacity (i.e. saturated, or not). Fifty years ago, many ecologists assumed dispersal was not limiting, and thus communities were saturated (e.g. [5,87]). Community saturation was a prerequisite for the hypothesis that patterns of diversity reflect the influence of the local physical environment on limits to species coexistence [88], and the foundation for analyses relating diversity to physical variation in the environment [89–93]. Observations of density compensation on islands and the effects of species removal experiments [94,95] show the power of interspecific competition. However, only species addition experiments can demonstrate whether ecological assemblages are filled with species, and such experiments are difficult from a logistical standpoint. Seeding experiments on North American grasslands [96,97] demonstrated that additional species could be packed into small areas, suggesting that local diversity is dispersal limited in the sense that the added species were regional natives. Similar conclusions derive from: (i) colonization experiments, in which habitats naturally colonized from a regional species pool vary in assemblage composition (e.g. [98,99]); (ii) analyses of multiple habitats (e.g. [28,29,100]), and (iii) exotic species invasions of undisturbed native assemblages without consistent competitive displacement of natives [101–104].

Increasingly, ecologists accept that local assemblages are not saturated with species, or at least that the degree of saturation is graded and without a firm upper limit. Evidence that exotic species often invade undisturbed native communities also leads one to question whether species with a long local evolutionary history necessarily are better adapted to local conditions than species that are introduced or colonize from elsewhere. Moreover, the number of exotic species tends to parallel that of native species, when viewed at coarse spatial scales, suggesting common suitability to all species of particular environments rather than repulsion of species from diverse assemblages; this is often referred to as the invasion paradox. Based on phylogenetic and biogeographic distributions of major clades of anuran amphibians, Wiens [37] suggests that abiotic tolerances are more important in biogeography than biotic interactions (competition and predation). This is consistent with the observation that recent avian colonists in the West Indies are generally more widespread and abundant than long-established endemics [105,106].

The transition from saturation-thinking to the idea of dispersal limitation occurred when modern ecology

finally returned to the ideas of H. A. Gleason [107] and R. H. Whittaker [108], namely that local habitats exist in a regional context, and so began reconsidering local habitats as open systems with a history [109–111]. As a result of this process, ecology began to converge towards biogeography, among whose basic tenets are that dispersal can be limiting and that history matters [112]. The continued recognition that dispersal limitation and historical conditions can affect species composition of local habitats will do much to bridge differences between ecology and biogeography. A major research question is to understand the spatial and temporal scales at which dispersal limitation matters, and conversely where and when it does not matter to local and regional communities. Besides being important for biogeography and ecology, this direction is essential to problems in applied ecology, in which conservation and restoration each depend on managing dispersal limitation (reducing limits for threatened species, increasing limits for invasive species) and historically informed resource management decisions (e.g. [113]).

9. DIVERSIFICATION AND THE DEVELOPMENT OF REGIONAL BIOTAS

With respect to the species saturation of communities, Wiens [37] makes the important point that assemblages of species from an older lineage are open to further invasion by more recent lineages. One presumes that any particular biota builds over time through evolutionary diversification and colonization. This impression is reinforced by phylogenetic analyses, which portray the relationships of contemporary species as coalescing back through time to a single common ancestor. What phylogenetic analysis fails to show, however, are the extinct lineages. In the case of large mammals that have a relatively well-resolved fossil record, species richness and phylogenetic diversity in South America (see [38]) increased substantially following the introduction of North American lineages in 'The Great American Interchange,' although many South American lineages dropped out. This approach is less satisfactory for taxa with weaker fossil records. For example, the fossil record for birds is poor, but South American avifaunas include large late-comer radiations of birds from North American stem lineages (e.g. wrens Troglodytidae, and tanagers Thraupidae). The wrens are intercalated morphologically and ecologically among the South American antbirds (Thamnophilidae), but the tanagers have the canopy fruit-eating niche practically to themselves [114]. Without a fossil record, one cannot determine whether tanagers drove endemic South American tanager-like lineages to extinction, or North American tanagers entered a conveniently empty niche.

Although lineage-through-time plots derived from phylogenetic reconstruction allow estimates of speciation and extinction rates [115–120], the critical assumption of rate constancy over time is rarely met. Instead diversification would appear to vary dramatically in response to mass extinctions and with changes in the environment (e.g. mammals [121],

whales [122]). Nonetheless, the fossil records of many taxa display relative constancy through long periods, including the whole of the Tertiary: tropical forest trees [123]; North American mammals [124]; diatoms [125] and marine invertebrates [126]. Evidence that the species richness of evolutionary clades is largely independent of age [127] suggests that the rate of diversification might be diversity dependent, and diversity might ultimately be limited by some regional carrying capacity for species [128–130]. Other studies, often at larger scales, support instead relatively constant rates of diversification over long periods [131,132], but this does not contradict a regional carrying capacity with constant turnover of species.

Although larger regions support larger clades [132,133] and augment local diversity [134–136], the mechanisms by which diversity feeds back on diversification are unclear. Steady-state diversity implies either that regions are fully packed ecologically, or that particular geographical configurations influence the position of the steady state, as argued by Qian & Ricklefs [137] for the greater plant diversity of temperate eastern Asia compared with eastern North America. Such diversity anomalies emphasize the contribution of regional processes to regional and local diversification. For example, modern lineages of mangrove plants have arisen, judging from first appearances in the fossil record, at a steady rate of one every four-to-five million years, but the transition between terrestrial ancestors and mangrove descendants has occurred almost entirely in the Old World, creating a substantial diversity anomaly between the hemispheres [58].

10. CONCLUSIONS

Recent progress in portraying the geography and history of life on Earth has been exhilarating! With the growing volume of data and sophistication of analysis, it is equally encouraging that ecologists and biogeographers are finding more common ground and are willing to entertain a wider range of explanations for perceived patterns. Recognizing that life occurs on a continuum, ranging from the activities of the individual over its lifetime to the global distribution of evolutionary lineages down through the history of the Earth adds complexity to an already difficult exercise, but also brings new possibilities for resolution. To some extent, the wealth of new data and analyses has merely substantiated older observations. For example, phylogenetic analyses of species sorting and niche partitioning have substantiated previous analyses based on taxonomic distinctions, including species-to-genus ratios [79]. Taxonomy was also sufficient to distinguish ancestry from convergence in many comparative studies of form and function across biogeographic realms [49].

New data and analyses have also added to the complexity of nature as we perceive it. Phylogenetic reconstructions have failed to provide a simple model of historical diversification, but have reinforced some old insights, such as diversity-dependent diversification [138,139], that require explanation. One of us (R.R.) has been much enamoured with the potential roles of pathogens in structuring ecological and

biogeographic patterns [47,140,141]. For example, whereas phylogenetic overdispersion has been attributed to competition and niche partitioning, pathogens might accomplish the same type of spatial segregation through apparent competition [142,143] being most intense among related hosts. Indeed, pathogen influence provides an alternative to the distinction of abiotic factors (species sorting) and biotic factors (niche partitioning), because host species carry their parasites with them. To the extent that parasites are specialized to their hosts [144], they add dimensions to the multi-dimensional niche space and promote coexistence because: (i) host–pathogen interactions evolve readily and thus can explain why most of the variance in distribution and abundance occurs between closely related species; (ii) pathogens might influence diversification by creating disease incompatibilities between isolated populations, on the one hand, and preventing secondary sympatry, on the other [145]; and (iii) to the extent that pathogens diversify with their hosts, they could support continued diversification of host lineages [141]. We raise the issue of pathogens because it exemplifies the broad range of possibilities that lie before us. We might never fully understand the distribution of biodiversity over the surface of the Earth, but exploration of the broad landscape of possibilities should continue to satisfy our curiosity about the world around us, motivate scientific inquiry, and contribute to a scientific basis for conservation of biodiversity.

REFERENCES

1 McIntosh, R. P. 1985 *The background of ecology: concept and theory.* Cambridge, UK: Cambridge University Press.
2 MacArthur, R. H. 1965 Patterns of species diversity. *Biol. Rev.* **40**, 510–533. (doi:10.1111/j.1469-185X.1965.tb00815.x)
3 MacArthur, R. H. 1972 *Geographical ecology: patterns in the distribution of species.* New York, NY: Harper and Row.
4 Kingsland, S. E. 1985 *Modeling nature: episodes in the history of population ecology.* Chicago, IL: University of Chicago Press.
5 MacArthur, R. H. & Wilson, E. O. 1963 An equilibrium theory of insular zoogeography. *Evolution* **17**, 373–387. (doi:10.2307/2407089)
6 MacArthur, R. H. & Wilson, E. O. 1967 *The theory of island biogeography.* Princeton, NJ: Princeton University Press.
7 Pianka, E. R. 1966 Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.* **100**, 33–46. (doi:10.1086/282398)

8 Janzen, D. H. 1970 Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528. (doi:10.1086/282687)
9 Connell, J. H. 1978 Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310. (doi:10.1126/science.199.4335.1302)
10 Colwell, R. K. & Lees, D. C. 2000 The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol. Evol.* **15**, 70–76. (doi:10.1016/S0169-5347(99)01767-X)
11 Colwell, R. K., Rahbek, C. & Gotelli, N. J. 2004 The mid-domain effect and species richness patterns: what have we learned so far? *Am. Nat.* **163**, E1–E23. (doi:10.1086/382056)
12 Hubbell, S. P. 2001 *The unified neutral theory of biodiversity and biogeography.* Princeton, NJ: Princeton University Press.
13 Chave, J. 2004 Neutral theory and community ecology. *Ecol. Lett.* **7**, 241–253. (doi:10.1111/j.1461-0248.2003.00566.x)
14 Croizat, L. 1958 *Panbiogeography or an introductory synthesis of zoogeography, phytogeography, geology.* Caracas, Venezuela: L. Croizat.
15 Wiley, E. O. 1988 Vicariance biogeography. *Annu. Rev. Ecol. Syst.* **19**, 513–542. (doi:10.1146/annurev.es.19.110188.002501)
16 Myers, A. A. & Giller, P. S. (eds) 1988 *Analytical biogeography: an integrated approach to the study of animal and plant distributions.* London, UK: Chapman and Hall.
17 Rapoport, E. H. 1982 *Aerography: geographical strategies of species.* Oxford, UK: Pergamon.
18 Brown, J. H. & Gibson, A. C. 1983 *Biogeography.* St. Louis, MO: Mosby.
19 Brown, J. H. & Maurer, B. A. 1989 Macroecology: the division of food and space among species on continents. *Science* **243**, 1145–1150. (doi:10.1126/science.243.4895.1145)
20 Brown, J. H. 1995 *Macroecology.* Chicago, IL: University of Chicago Press.
21 Gaston, K. J. & Blackburn, T. M. 2000 *Pattern and process in macroecology.* Oxford, UK: Blackwell Science.
22 Jenkins, D. G. & Ricklefs, R. E. 2011 Biogeography and ecology: two views of one world. *Phil. Trans. R. Soc. B* **366**, 2331–2335. (doi:10.1098/rstb.2011.0064)
23 Chase, J. M. & Leibold, M. A. 2003 *Ecological niches linking classical and contemporary approaches.* Chicago, IL: University of Chicago Press.
24 Soberón, J. 2007 Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* **10**, 1115–1123. (doi:10.1111/j.1461-0248.2007.01107.x)
25 Ricklefs, R. E. 2008 Disintegration of the ecological community. *Am. Nat.* **172**, 741–750. (doi:10.1086/593002)
26 Holt, R. D. 2009 Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc. Natl Acad. Sci. USA* **106**, 19 659–19 665. (doi:10.1073/pnas.0905137106)
27 Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T. & Bentivenga, S. 2011 Advances, challenges, and a developing synthesis of ecological community assembly theory. *Phil. Trans. R. Soc. B* **366**, 75–85. (doi:10.1098/rstb.2011.0056)
28 Jenkins, D. G. 2006 In search of quorum effects in metacommunity structure: species co-occurrence analyses. *Ecology* **87**, 1523–1531. (doi:10.1890/0012-9658(2006)87[1523:ISOQEI]2.0.CO;2)
29 Jenkins, D. G. 2011 Ranked species occupancy curves reveal common patterns among diverse metacommunities. *Glob. Ecol. Biogeogr.* **20**, 486–497. (doi:10.1111/j.1466-8238.2010.00617.x)

30 Morin, P. 1999 *Community ecology.* Oxford, UK: Blackwell Science.

31 Wilson, D. S. 1992 Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* **73**, 1984–2000. (doi:10.2307/1941449)

32 Leibold, M. A. *et al.* 2004 The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* **7**, 601–613. (doi:10.1111/j.1461-0248.2004.00608.x)

33 Chiarucci, A., Bacaro, G. & Scheiner, S. M. 2011 Old and new challenges in using species diversity for assessing biodiversity. *Phil. Trans. R. Soc. B* **366**, 98–109. (doi:10.1098/rstb.2011.0065)

34 Chase, J. M. & Myers, J. A. 2011 Disentangling the importance of ecological niches from stochastic processes across scale. *Phil. Trans. R. Soc. B* **366**, 23–35. (doi:10.1098/rstb.2011.0063)

35 Fauth, J. E., Bernardo, J., Camara, M., Resetarits Jr, W. J., Van Buskirk, J. & McCollum, S. A. 1996 Simplifying the jargon of community ecology: a conceptual approach. *Am. Nat.* **147**, 282–286. (doi:10.1086/285850)

36 Hutchinson, G. E. 1957 Concluding remarks. *Cold Spring Harbor Symp. Q. Biol.* **22**, 415–427. (doi:10.1101/SQB.1957.022.01.039)

37 Wiens, J. J. 2011 The niche, biogeography and species interactions. *Phil. Trans. R. Soc. B* **366**, 8–22. (doi:10.1098/rstb.2011.0059)

38 Davies, T. J. & Buckley, L. B. 2011 Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Phil. Trans. R. Soc. B* **366**, 86–97. (doi:10.1098/rstb.2011.0058)

39 Smith, F. A. & Lyons, S. K. 2011 How big should a mammal be? A macroecological look at mammalian body size over space and time. *Phil. Trans. R. Soc. B* **366**, 36–50. (doi:10.1098/rstb.2011.0067)

40 Emerson, B. C., Cicconardi, F., Fanciulli, P. P. & Shaw, P. J. A. 2011 Phylogeny, phylogeography, phylobetadiversity and the molecular analysis of biological communities. *Phil. Trans. R. Soc. B* **366**, 63–74. (doi:10.1098/rstb.2011.0057)

41 Poulin, R., Krasnov, B. R., Mouillot, D. & Thieltges, D. W. 2011 The comparative ecology and biogeography of parasites. *Phil. Trans. R. Soc. B* **366**, 51–62. (doi:10.1098/rstb.2011.0048)

42 Tuomisto, H. 2010 A diversity of beta diversities: straightening up a concept gone awry. I. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* **33**, 2–22. (doi:10.1111/j.1600-0587.2009.05880.x)

43 Tuomisto, H. 2010 A diversity of beta diversities: straightening up a concept gone awry. II. Quantifying beta diversity and related phenomena. *Ecography* **33**, 23–45. (doi:10.1111/j.1600-0587.2009.06148.x)

44 Carroll, S. P., Hendry, A. P., Reznick, D. N. & Fox, C. W. 2007 Evolution on ecological time-scales. *Funct. Ecol.* **21**, 387–393. (doi:10.1111/j.1365-2435.2007.01289.x)

45 Gaston, K. J. 1998 Species-range size distributions: products of speciation, extinction and transformation. *Phil. Trans. R. Soc. Lond. B* **353**, 219–230. (doi:10.1098/rstb.1998.0204)

46 Ricklefs, R. E. 2009 Speciation, extinction, and diversity. In *Speciation and patterns of diversity* (eds F. Butlin, J. Bridle & D. Schluter), pp. 257–277. Cambridge, UK: Cambridge University Press.

47 Ricklefs, R. E. 2010 Evolutionary diversification, coevolution between populations and their antagonists, and

48 Medley, K. A. 2010 Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. *Glob. Ecol. Biogeogr.* **19**, 122–133. (doi:10.1111/j.1466-8238.2009.00497.x)

49 Cody, M. L. & Mooney, H. A. 1978 Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annu. Rev. Ecol. Syst.* **9**, 265–321. (doi:10.1146/annurev.es.09.110178.001405)

50 Schluter, D. & Ricklefs, R. E. 1993 Convergence and the regional component of species diversity. In *Species diversity in ecological communities historical and geographical perspectives* (eds R. E. Ricklefs & D. Schluter), pp. 230–242. Chicago, IL: University of Chicago Press.

51 Samuels, C. L. & Drake, J. A. 1997 Divergent perspectives on community convergence. *Trends Ecol. Evol.* **12**, 427–432. (doi:10.1016/S0169-5347(97)01182-8)

52 Ricklefs, R. E. & Latham, R. E. 1992 Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *Am. Nat.* **139**, 1305–1321. (doi:10.1086/285388)

53 Sauer, J. D. 1988 *Plant migration the dynamics of geographic patterning in seed plant species.* Berkeley, CA: University of California Press.

54 Latham, R. E. & Ricklefs, R. E. 1993 Continental comparisons of temperate-zone tree species diversity. In *Species diversity in ecological communities. historical and geographical perspectives* (eds R. E. Ricklefs & D. Schluter), pp. 294–314. Chicago, IL: University of Chicago Press.

55 Svenning, J. C. 2003 Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecol. Lett.* **6**, 646–653. (doi:10.1046/j.1461-0248.2003.00477.x)

56 Ricklefs, R. E. & Latham, R. E. 1993 Global patterns of diversity in mangrove floras. In *Species diversity in ecological communities. historical and geographical perspectives* (eds R. E. Ricklefs & D. Schluter), pp. 215–229. Chicago, IL: University of Chicago Press.

57 Ellison, A. M., Farnsworth, E. J. & Merkt, R. E. 1999 Origins of mangrove ecosystems and the mangrove biodiversity anomaly. *Glob. Ecol. Biogeogr. Lett.* **8**, 95–115.

58 Ricklefs, R. E., Schwarzbach, A. E. & Renner, S. S. 2006 Rate of lineage origin explains the diversity anomaly in the world's mangrove vegetation. *Am. Nat.* **168**, 805–810. (doi:10.1086/508711)

59 Hawkins, B. A., Rodríguez, M. Á. & Weller, S. G. 2011 Global angiosperm family richness revisited: linking ecology and evolution to climate. *J. Biogeogr.* **38**. (doi:10.1111/j.1365-2699.2011.02490.x)

60 Judd, W. S., Sanders, R. W. & Donoghue, M. J. 1994 Angiosperm family pairs: preliminary phylogenetic analyses. *Harv. Pap. Bot.* **5**, 1–51.

61 Latham, R. E. & Ricklefs, R. E. 1993 Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos* **67**, 325–333. (doi:10.2307/3545479)

62 Wiens, J. J. & Donoghue, M. J. 2004 Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* **19**, 639–644. (doi:10.1016/j.tree.2004.09.011)

63 Ricklefs, R. E. 2005 Phylogenetic perspectives on patterns of regional and local species richness. In *Tropical rainforests: past, present, and future* (eds E. Bermingham, C. W. Dick & C. Moritz), pp. 16–40. Chicago, IL: University of Chicago Press.

64 Ricklefs, R. E. 2006 Evolutionary diversification and the origin of the diversity/ environment relationship.

Ecology **87**, S3–S13. (doi:10.1890/0012-9658(2006)87
[3:EDATOO]2.0.CO;2)

65 Diniz-Fihlo, J. A., Rangel, T. F., Bini, L. M. & Hawkins,
B. A. 2007 Macroevolutionary dynamics of species in
environmental space and the latitudinal diversity gradi-
ent in New World birds. *Proc. R. Soc. B* **274**, 43–52.
(doi:10.1098/rspb.2006.3712)

66 Hawkins, B. A., Diniz-Filho, J. A. F., Jaramillo, C. A. &
Soeller, S. A. 2007 Climate, niche conservatism, and
the global bird diversity gradient. *Am. Nat.* **170**,
S16–S27. (doi:10.1086/519009)

67 Hawkins, B. A. & DeVries, P. J. 2009 Tropical
niche conservatism and the species richness gradient
of North American butterflies. *J. Biogeogr.* **36**,
1698–1711. (doi:10.1111/j.1365-2699.2009.02119.x)

68 Buckley, L. B. *et al.* 2010 Phylogeny, niche conserva-
tism, and the latitudinal diversity gradient in
mammals. *Proc. R. Soc. B* **277**, 2131–2138. (doi:10.
1098/rspb.2010.0179)

69 Webb, S. D. 1976 Mammalian faunal dynamics
of the Great American Interchange. *Paleobiology* **2**,
220–234.

70 Marshall, L. G., Webb, S. D., Sepkoski Jr, J. J. &
Raup, D. M. 1982 Mammalian evolution and the
Great American Interchange. *Science* **215**, 1351–1357.
(doi:10.1126/science.215.4538.1351)

71 Webb, S. D. 1991 Ecogeography and the Great
American Interchange. *Paleobiology* **17**, 266–280.

72 Houle, A. 1999 The origin of platyrrhines: an evalu-
ation of the Antarctic scenario and the floating island
model. *Am. J. Phys. Anthropol.* **109**, 541–559. (doi:10.
1002/(SICI)1096-8644(199908)109:4<541::AID-AJP
A9>3.0.CO;2-N)

73 Takai, M., Anaya, F., Shigehara, N. & Setoguchi, T.
2000 New fossil materials of the earliest New World
monkey, *Branisella boliviana*, and the problem of platyr-
rhine origins. *Am. J. Phys. Anthropol.* **111**, 263–281.
(doi:10.1002/(SICI)1096-8644(200002)111:2<263::
AID-AJPA10>3.0.CO;2-6)

74 Huchon, D. E. & Douzery, J. P. 2001 From the Old
World to the New World: a molecular chronicle of the
phylogeny and biogeography of hystricognath rodents.
Mol. Phylogenet. Evol. **20**, 238–251. (doi:10.1006/
mpev.2001.0961)

75 Opazo, J. C. 2005 A molecular timescale for Cavio-
morph rodents (Mammalia, Hystricognathi). *Mol.
Phylogenet. Evol.* **37**, 932–937. (doi:10.1016/j.ympev.
2005.05.002)

76 Renner, S. S. 2004 Tropical trans-Atlantic disjunctions,
sea surface currents, and wind patterns. *Int. J. Plant Sci.*
165, S23–S33. (doi:10.1086/383334)

77 Hawkins, B. A., Diniz, J. A. F., Jaramillo, C. A. &
Soeller, S. A. 2006 Post-Eocene climate change, niche
conservatism, and the latitudinal diversity gradient of
New World birds. *J. Biogeogr.* **33**, 770–780. (doi:10.
1111/j.1365-2699.2006.01452.x)

78 Webb, C. O. 2000 Exploring the phylogenetic structure
of ecological communities: an example for rain forest
trees. *Am. Nat.* **156**, 145–155. (doi:10.1086/303378)

79 Webb, C. O., Ackerly, D. D., McPeek, M. A. &
Donoghue, M. J. 2002 Phylogenies and community
ecology. *Annu. Rev. Ecol. Syst.* **33**, 475–505. (doi:10.
1146/annurev.ecolsys.33.010802.150448)

80 Cavender-Bares, J., Ackerly, D. D., Baum, D. A. &
Bazzaz, F. A. 2004 Phylogenetic overdispersion in
Floridian oak communities. *Am. Nat.* **163**, 823–843.
(doi:10.1086/386375)

81 Cavender-Bares, J., Keen, A. & Miles, B. 2006
Phylogenetic structure of Floridian plant communities
depends on taxonomic and spatial scale. *Ecology* **87**,
S109–S122. (doi:10.1890/0012-9658(2006)87[109:
PSOFPC]2.0.CO;2)

82 Kraft, N. J. B., Cornwell, W. K., Webb, C. O. & Ackerly,
D. D. 2007 Trait evolution, community assembly, and
the phylogenetic structure of ecological communities.
Am. Nat. **170**, 271–283. (doi:10.1086/519400)

83 Johnson, M. T. J. & Stinchcombe, J. R. 2007 An emer-
ging synthesis between community ecology and
evolutionary biology. *Trends Ecol. Evol.* **22**, 250–257.
(doi:10.1016/j.tree.2007.01.014)

84 Emerson, B. C. & Gillespie, R. G. 2008 Phylogenetic
analysis of community assembly and structure over
space and time. *Trends Ecol. Evol.* **23**, 619–630.
(doi:10.1016/j.tree.2008.07.005)

85 Cavender-Bares, J., Kozak, K., Fine, P. & Kembel, S.
2009 The merging of community ecology and phylo-
genetic biology. *Ecol. Lett.* **12**, 693–715. (doi:10.1111/
j.1461-0248.2009.01314.x)

86 Vamosi, S. M., Heard, S. B., Vamosi, J. C. & Webb,
C. O. 2009 Emerging patterns in the comparative
analysis of phylogenetic community structure. *Mol.
Ecol.* **18**, 572–592. (doi:10.1111/j.1365-294X.2008.
04001.x)

87 Lack, D. 1976 *Island biology illustrated by the land
birds of Jamaica*. Berkeley, CA: University of California
Press.

88 Mittelbach, G. G. *et al.* 2007 Evolution and the latitu-
dinal diversity gradient: speciation, extinction and
biogeography. *Ecol. Lett.* **10**, 315–331. (doi:10.1111/j.
1461-0248.2007.01020.x)

89 Currie, D. J. 1991 Energy and large scale patterns
of animal and plant species richness. *Am. Nat.* **137**,
27–49. (doi:10.1086/285144)

90 O'Brien, E. M. 1998 Water-energy dynamics, climate,
and prediction of woody plant species richness—an
interim general model. *J. Biogeogr.* **25**, 379–398.
(doi:10.1046/j.1365-2699.1998.252166.x)

91 O'Brien, E. M., Field, R. & Whittaker, R. J. 2000
Climatic gradients in woody plant (tree and shrub)
diversity: water-energy dynamics, residual variation,
and topography. *Oikos* **89**, 588–600. (doi:10.1034/j.
1600-0706.2000.890319.x)

92 Hawkins, B. A. *et al.* 2003 Energy, water, and broad-
scale geographic patterns of species richness. *Ecology*
84, 3105–3117. (doi:10.1890/03-8006)

93 Kreft, H. & Jetz, W. 2007 Global patterns and determin-
ants of vascular plant diversity. *Proc. Natl Acad. Sci. USA*
104, 5925–5930. (doi:10.1073/pnas.0608361104)

94 Schoener, T. W. 1983 Field experiments on interspecific
competition. *Am. Nat.* **122**, 240–285. (doi:10.1086/
284133)

95 Díaz, S., Symstad, A. J., Chapin, F. S., Wardle, D. A. &
Huenneke, L. F. 2003 Functional diversity revealed by
removal experiments. *Trends Ecol. Evol.* **18**, 140–146.
(doi:10.1016/S0169-5347(03)00007-7)

96 Tilman, D. 1997 Community invasibility, recruitment
limitation, and grassland biodiversity. *Ecology* **78**,
81–92. (doi:10.1890/0012-9658(1997)078[0081:CIR
LAG]2.0.CO;2)

97 Houseman, G. R. & Gross, K. L. 2011 Linking grass-
land plant diversity to species pools, sorting and plant
traits. *J. Ecol.* **99**, 464–472.

98 McCune, B. & Allen, T. F. H. 1985 Will similar forests
develop on similar sites? *Can. J. Bot.* **63**, 367–376.
(doi:10.1139/b85-043)

99 Jenkins, D. G. & Buikema Jr, A. L. 1998 Do similar
communities develop in similar sites? A test with zoo-
plankton structure and function. *Ecol. Monogr.* **68**,
421–443. (doi:10.1890/0012-9615(1998)068[0421:
DSCDIS]2.0.CO;2)

100 Ng, I. S. Y., Carr, C. & Cottenie, K. 2009 Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia* **619**, 133–143. (doi:10.1007/s10750-008-9605-8)

101 Gurevitch, J. & Padilla, D. K. 2004 Are invasive species a major cause of extinctions? *Trends Ecol. Evol.* **19**, 470–474. (doi:10.1016/j.tree.2004.07.005)

102 MacDougall, A. S. & Turkington, R. 2005 Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**, 42–55. (doi:10.1890/04-0669)

103 Sax, D. F. *et al.* 2007 Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol.* **22**, 465–471. (doi:10.1016/j.tree.2007.06.009)

104 Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., Stohlgren, T. J., Tilman, D. & Von Holle, B. 2007 The invasion paradox: reconciling pattern and process in species invasions. *Ecology* **88**, 3–17. (doi:10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2)

105 Ricklefs, R. E. & Cox, G. W. 1978 Stage of taxon cycle, habitat distribution, and population density in the avifauna of the West Indies. *Am. Nat.* **112**, 875–895. (doi:10.1086/283329)

106 Ricklefs, R. E. & Bermingham, E. 2002 The concept of the taxon cycle in biogeography. *Glob. Ecol. Biogeogr.* **11**, 353–361. (doi:10.1046/j.1466-822x.2002.00300.x)

107 Gleason, H. A. 1926 The individualistic concept of the plant association. *Torrey Bot. Club Bull.* **53**, 7–26.

108 Whittaker, R. H. 1953 A consideration of climax theory: the climax as a population and pattern. *Ecol. Monogr.* **23**, 41–78.

109 Ricklefs, R. E. 1987 Community diversity: relative roles of local and regional processes. *Science* **235**, 167–171. (doi:10.1126/science.235.4785.167)

110 Roughgarden, J., Gaines, S. & Pacala, S. 1987 Supply side ecology: the role of physical transport processes. In *Organization of communities, past and present. The 27th Symp. of the British Ecological Society* (eds J. H. R. Gee & P. S. Giller), pp. 491–518. London, UK: Blackwell Scientific.

111 Ricklefs, R. E. & Schluter, D. (eds) 1993 *Species diversity in ecological communities*. Chicago, IL: University of Chicago Press.

112 Lomolino, M. V., Riddle, B. R., Whittaker, R. J. & Brown, J. H. 2010 *Biogeography*, 4th edn. Sunderland, MA: Sinauer Associates.

113 Foster, B. L., Murphy, C. A., Keller, K. A., Aschenbach, T. A., Questad, E. J. & Kindscher, K. 2007 Restoration of prairie community structure and ecosystem function in an abandoned hayfield: a sowing experiment. *Restor. Ecol.* **5**, 652–661. (doi:10.1111/j.1526-100X.2007.00277.x)

114 Ricklefs, R. E. 2002 Splendid isolation: historical ecology of the South American passerine fauna. *J. Avian Biol.* **33**, 207–211. (doi:10.1034/j.1600-048X.2002.330301.x)

115 Nee, S., Mooers, A. O. & Harvey, P. H. 1992 Tempo and mode of evolution revealed from molecular phylogenies. *Proc. Natl Acad. Sci. USA* **89**, 8322–8326. (doi:10.1073/pnas.89.17.8322)

116 Harvey, P. H., May, R. M. & Nee, S. 1994 Phylogenies without fossils. *Evolution* **48**, 523–529. (doi:10.2307/2410466)

117 Nee, S., Holmes, E. C., May, R. M. & Harvey, P. H. 1994 Extinction rates can be estimated from molecular phylogenies. *Phil. Trans. R. Soc. Lond. B* **344**, 77–82. (doi:10.1098/rstb.1994.0054)

118 Nee, S., May, R. M. & Harvey, P. H. 1994 The reconstructed evolutionary process. *Phil. Trans. R. Soc. Lond. B* **344**, 305–311. (doi:10.1098/rstb.1994.0068)

119 Nee, S. 2006 Birth-death models in macroevolution. *Annu. Rev. Ecol. Evol. Syst.* **37**, 1–17. (doi:10.1146/annurev.ecolsys.37.091305.110035)

120 Ricklefs, R. E. 2007 Estimating diversification rates from phylogenetic information. *Trends Ecol. Evol.* **22**, 601–610. (doi:10.1016/j.tree.2007.06.013)

121 Bininda-Emonds, O. R. P. *et al.* 2007 The delayed rise of present-day mammals. *Nature* **446**, 507–512. (doi:10.1038/nature05634)

122 Steeman, M. E. *et al.* 2009 Radiation of extant cetaceans driven by restructuring of the oceans. *Syst. Biol.* **58**, 573–585. (doi:10.1093/sysbio/syp060)

123 Jaramillo, C., Rueda, M. J. & Mora, G. 2006 Cenozoic plant diversity in the Neotropics. *Science* **311**, 1893–1896. (doi:10.1126/science.1121380)

124 Alroy, J. 2000 Successive approximations of diversity curves: ten more years in the library. *Geology* **28**, 1023–1026. (doi:10.1130/0091-7613(2000)28<1023:SAODCT>2.0.CO;2)

125 Rabosky, D. L. & Sorhannus, U. 2009 Diversity dynamics of marine planktonic diatoms across the Cenozoic. *Nature* **457**, 183–186. (doi:10.1038/nature07435)

126 Alroy, J. *et al.* 2008 Phanerozoic trends in the global diversity of marine invertebrates. *Science* **321**, 97–100. (doi:10.1126/science.1156963)

127 Ricklefs, R. E. 2006 Global variation in the diversification rate of passerine birds. *Ecology* **87**, 2468–2478. (doi:10.1890/0012-9658(2006)87[2468:GVITDR]2.0.CO;2)

128 Rabosky, D. L. & Lovette, I. J. 2008 Density-dependent diversification in North American wood warblers. *Proc. R. Soc. B* **275**, 2363–2371. (doi:10.1098/rspb.2008.0630)

129 Rabosky, D. L. & Lovette, I. J. 2008 Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution* **62**, 1866–1875. (doi:10.1111/j.1558-5646.2008.00409.x)

130 Rabosky, D. L. 2009 Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecol. Lett.* **12**, 735–743. (doi:10.1111/j.1461-0248.2009.01333.x)

131 Linder, H. P. 2005 Evolution of diversity: the Cape flora. *Trends Plant Sci.* **10**, 536–541. (doi:10.1016/j.tplants.2005.09.006)

132 Ricklefs, R. E. 2006 The unified neutral theory of biodiversity: do the numbers add up? *Ecology* **87**, 1424–1431. (doi:10.1890/0012-9658(2006)87[1424:TUNTOB]2.0.CO;2)

133 Ricklefs, R. E. 2007 History and diversity: explorations at the intersection of ecology and evolution. *Am. Nat.* **170**, S56–S70.

134 Hugueny, B., Demorais, L. T., Merigoux, S., Demerona, B. & Ponton, D. 1997 The relationship between local and regional species richness: comparing biotas with different evolutionary histories. *Oikos* **80**, 583–587. (doi:10.2307/3546633)

135 Srivastava, D. 1999 Using local-regional richness plots to test for species saturation: pitfalls and potentials. *J. Anim. Ecol.* **68**, 1–16. (doi:10.1046/j.1365-2656.1999.00266.x)

136 Loreau, M. 2000 Are communities saturated? On the relationship between α, β, and γ diversity. *Ecol. Lett.* **3**, 73–76. (doi:10.1046/j.1461-0248.2000.00127.x)

137 Qian, H. & Ricklefs, R. E. 2000 Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature* **407**, 180–182. (doi:10.1038/35025052)

138 Raup, D. M. & Gould, S. J. 1974 Stochastic simulation and evolution of morphology—towards a nomothetic paleontology. *Syst. Zool.* **23**, 305–322. (doi:10.2307/2412538)

139 Stanley, S. M. 1979 *Macroevolution: pattern and process.* San Francisco, CA: W. H. Freeman.

140 Ricklefs, R. E. 2010 Host–pathogen coevolution, secondary sympatry, and species diversification. *Phil. Trans. R. Soc. B* **365**, 1139–1147. (doi:10.1098/rstb.2009.0279)

141 Ricklefs, R. E. 2011 A biogeographic perspective on ecological systems: some personal reflections. *J. Biogeogr.* (doi:10.1111/j.1365-2699.2011.02520.x)

142 Holt, R. D. 1977 Predation, apparent competition, and the structure of prey communities. *Theoret. Popul. Biol.* **12**, 197–229. (doi:10.1016/0040-5809(77)90042-9)

143 Holt, R. D. & Lawton, J. H. 1994 The ecological consequences of shared natural enemies. *Annu. Rev. Ecol. Syst.* **25**, 495–520. (doi:10.1146/annurev.es.25.110194.002431)

144 Poulin, R. 2007 *Evolutionary ecology of parasites*, 2nd edn. Princeton, NJ: Princeton University Press.

145 Ricklefs, R. E. & Bermingham, E. 2007 The causes of evolutionary radiations in archipelagoes: passerine birds in the Lesser Antilles. *Am. Nat.* **169**, 285–297. (doi:10.1086/510730)